Colony survivorship of social caterpillars in the field: A case study of the small eggar moth (Lepidoptera: Lasiocampidae)

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Abstract: We investigated survivorship of 100 caterpillar colonies of the tent-building central place-foraging moth, *Eriogaster lanestris.* Our aim was to demonstrate if survival patterns match those reported for the related eastern tent caterpillar, *Malacosoma americanum,* which has a similar social system. The field experiment took place at four sites in northern Bavaria, Germany, in May and June 2002. Egg clusters were obtained from females mated in the laboratory and were exposed in the field just before hatching of the young caterpillars. Establishment of larval tents and survivorship on the colony level was then monitored until completion of larval development. In total, 52% of colonies had at least one larva surviving until pupation, with no significant differences between the four study sites. Colony-level mortality rate was constant over time and did not drop markedly during the last two larval instars, when *E. lanestris* larvae develop urticating hairs that are presumed to confer protection against vertebrate predators. The inability to build an initial tent, or the later loss of the tent, accounted for 71% of the observed total colony losses. Strong rainfall had a severe influence on the constitution of tents and increased the likelihood of colony failure. Overall, maintenance of an intact tent emerged as the single most important predictor of colony survival.

Key words: colony survivorship, *Eriogaster lanestris,* Germany, predation, rainfall, tent-building caterpillars

Introduction

Lepidopteran larvae are most vulnerable in the earliest stages of their lives. Natural enemies are often the dominant cause of mortality (Cornell et al. 1998). Only few Lepidopteran caterpillars (<3% of the species worldwide, Costa & Pierce 1997) live gregariously or 'socially', sometimes in groups of several hundreds of individuals. Gregarious caterpillars may benefit from living in groups, for example by maximizing growth through efficient thermoregulation (Joos et al. 1988; Ruf & Fiedler 2000, 2002b) or by social feeding facilitation (Clark & Faeth 1997; Denno & Benrey 1997). However, since they are very conspicuous at the same time, caterpillar groups may incur a high risk of predation once they have been detected by visually hunting predators like birds, or by predators that recruit further nest-mates to food (e.g. ants, wasps).

Many gregarious species show warning coloration (Sillén-Tullberg 1988; Vulinec 1990) and are suggested to be chemically or structurally defended, which enables them to behave conspicuously (Heinrich 1979, 1993). The effect of aposematism may be enhanced by gregarious life habits because grouping renders the aposematic signal more effective by generating a greater aversion in predators (Gamberale & Tullberg 1996, 1998). Nevertheless, unless unpalatability is tested explicitly for any species an assumption of chemical defense always remains doubtful. In addition, the effectiveness of any defensive structures may vary according to the larval stage as well as between various types of predators.

We here study larval survivorship of the tent-building small eggar moth, *Eriogaster lanestris* (Linnaeus 1758) under the influence of natural predation and adverse

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weather conditions. *E. lanestris* caterpillars hatch in spring a few days after budbreak. They live together in and on a silken tent until the very end of their develop-ment, when they finally leave the tent and pupate some meters away (Ruf et al. 2003). Females lay all their eggs in one single cluster and siblings stay together for their whole development. Caterpillars start building the tent right after hatching, and expand it throughout development. Tents may achieve a volume of 750cm³. Since the tent does not include any resources, caterpillars must leave it for every food intake, i.e. they are central-place foragers according to Fitzgerald & Peterson (1988). Individuals are highly site tenacious and always return to the tent after feeding even if this has been severely damaged. Young caterpillars (L1-L3) are totally black (to the human observer) and bear white setae, whereas fourth instar caterpillars develop additional tufts of shorter red urticating hairs, which become even more pronounced in the fifth (last) instar.

Various aspects of group living in *E. lanestris* have been analyzed in recent years, but mostly in the laboratory (Ruf & Fiedler 2000, 2002a, b; Ruf et al. 2001a). Data on the survival of caterpillars in the field are crucial for understanding the costs associated with sociality in this species, since the destruction of a colony means the total loss of a female's offspring. We here investigate survivorship in *E. lanestris* at the colony level under field conditions, with special reference to the timing and impact of predation as well as to the effects of heavy rainfall. In line with earlier findings by Costa (1993) on the related Eastern tent caterpillar, *Malacosoma americanum* (Fabricius 1793), and in view of the development of advanced chemical defense (= urticating hairs) in older instars of *E. lanestris* we expected mortality to be highest in young instars (especially before a tent has been fully established) and to level off when caterpillars approach maturity.

MATERIAL AND METHODS

Study sites

Study sites (Table 1) were situated in the region around Bayreuth (Germany, northern Bavaria). All were xerothermic habitats on limestone with blackthorn (*Prunus spinosa* Linnaeus, Rosaceae) bushes and/or hedgerows. At sites HP and PB we found naturally occurring tents of *E. lanestris* several times between 1999 and 2002. The site HL had previously been only scarcely covered with blackthorn bushes but presently blackthorn shrubs rapidly spread over the whole site. The site BB is a former military training area managed through regular grazing by sheep and goats but also experiences massive encroachment by blackthorn. For BB the occurrence of *E. lanestris* was reported for at least the end of the 1970s (Wolf 1982).

Animals

One-hundred egg clusters laid on small twigs were attached between 8-10 May with small pieces of wire to branches of blackthorn, a preferred natural host-plant in southern Germany (Ebert 1994). We chose the top of smaller bushes (height <ca. 1.7 m) or the sun-exposed side of higher plants (height 2-3 m). Egg clusters were placed 0.5-1.5 m above ground (depending on the height of the plant) and were marked with small numbered labels for later relocation and identification. The number of egg clusters exposed per site varied (Table 1) depending on the size of the area and the availability of suitable blackthorns. All egg clusters stemmed from a laboratory bred stock (third laboratory generation, original animals from site HP).

Monitoring and acquisition of data

After exposure of egg masses at the field sites hatching of the caterpillars and development was monitored once a week (Table 2). Due to the distance between sites, it was not possible to census all sites at one day. Experimental egg clusters were not attached to the blackthorns before budbreak to prevent caterpillars from hatching too early. Two naturally occurring field colonies (sites HP and HL) were one larval stage ahead at the onset of the experiment. Nevertheless, some experimental colonies finished development before the younger one of the natural colonies. Thus, experimental colonies were largely synchronous with the natural populations and experienced predation and weather in much the same way as these.

We here focus on colony, rather than individual, survivorship since even under high solar irradiation usually only a fraction of colony members can be observed on or outside the tent (Ruf & Fiedler 2002b). Moreover, the proportion of larvae active outside the tent strongly varies during molting

Table 1. Study sites, numbers of exposed *Eriogaster lanestris* egg masses, and survivorship of colonies during a field experiment in May and June 2002 in northern Bavaria, Germany.

Site	Latitude	Longitude	Altitude (m)	Exposure	Colonies surviving to 5th instar/ total number exposed	Proportion colonies surviving
BB	49°59′40′′	11°38′00′′	490	SW and plateau	22 / 5	44%
HP	49°48′50′′	11°26′50′′	615	plateau	10 / 15	67%
PB	49°46′40′′	11°27′10′′	460	S	9 / 15	60%
HL	49°48′20′′	11°24′20′′	560	SW	11 / 20	55%
Total					52 / 100	52%

Table 2. Exposure dates, census dates and progress of larval development for 100 experimental *E. lanestris* colonies.

	Site BB		Site HP, HL, PB	
Start	8-9 May	exposure	10 May	exposure
Census 1	15 May	first caterpillars hatched	20 May	60% of colonies hatched
Census 2	22 May	L1, most tents established	26 May	L1, most tents established
Census 3	28 May	L1/L2	1 June	L1/L2
Census 4	4 June	L2/L3	9 June	L2/L3
Census 5	12 June	L2-L4 (most L3)	16 June	L2-L4 (most L3)
Census 6	19 June	L3-L5 (most L4)	22 June	L3-L5 (most L4)
Census 7	26 June	most tents abandoned	29 June	L5 or abandoned

Table 3. Descriptors for the condition of colonies (pertinent to either egg cluster or tent).

Descriptor	Explanation
hatched	caterpillars just hatched, no tent yet established
infertile	no caterpillars hatched from the egg clusters within three weeks
no tent	caterpillars without tent (just after hatching, because of small number of caterpillars, or after destruction of tent)
intact	tent with no physical damage
repaired	tent was obviously damaged, but new silk has been spread over the holes
damaged	egg cluster: parts are missing; tent: shows holes, not yet repaired
destroyed	egg cluster: no eggs left; tent: completely destroyed, but caterpillars still alive
abandoned	tent abandoned, occasionally fifth (=final) instar caterpillars in the nearby surroundings
extinct	colony completely destroyed, no caterpillars nearby

Table 4. Monthly mean temperature and mean sum of precipitation in Bayreuth (northern Bavaria, Germany) in May and June between 1971 and 2001, and in the year of the study.

	May 1971-2001	June 1971-2001	May 2002	June 2002
Temperature [°C]	12.0	14.9	14.1	17.5
Sum of precipitation [mm]	56.3	78.9	76.5	113.4

periods (Ruf et al. 2001b). Thus, a reliable census of tent-mates cannot be achieved without severely damaging the colony.

The condition of colonies was evaluated using the descriptors listed in Table 3. If possible, the cause of the damage of a tent was recorded. Predation by invertebrates does not leave obvious marks on the tent. Predation by birds leaves large holes inmidst the silk mats of the tent. Damage caused by rain is clearly distinguishable from that by birds since ruptures due to rain arise from the edges of the mats and stretch in the direction of the silk filaments.

Climatic data were provided by the meteorological station at Bayreuth University (49°55'45"N 11°35'10"E, 365m asl). These data depict the regional weather conditions during the time of the study (all study sites are less than 20km away from the station). Minor local variation in temperature or the extent of rainfall was not considered.

Results

During the period of observations, mean daytime temperature (7a.m.-7.p.m.) was 18.9°C, mean nighttime temperature (9p.m.-5a.m.) was 11.3°C. Maximum temperature was 33.0°C and nighttime minimum temperature was always above 0°C (minimum: 2.8°C) (Fig. 1). Mean temperature and the sum of precipitation were higher in May and June 2002 compared to the average of the last 30 years (Table 4). On June 6 unusually strong rainfall occurred with 43l/m²×h. Compared to other years (1992-2001) the monthly sum of rainfall varied considerably among years but such extreme rainfall events in May and June are exceptionally rare in the study region (Ruf 2003).

Most caterpillars hatched between May 15 and May 20 (about one week after exposure in the field) and left their tents around the end of June (colonies at site BB a few days ahead compared to the colonies at the sites HL, HP, and PB). Thus, the complete development of the caterpillars lasted approximately 6-7 weeks (caterpillars pupate very soon after leaving the tent: C. Ruf, *pers. obs.*).

Five of 100 egg-batches failed to eclose. Obviously, these eggs were not fertile. Two egg clusters disappeared prior to hatching from unknown reasons. In 94.2% of all colonies that were successful in building a tent (N=69), the tent was directly built on

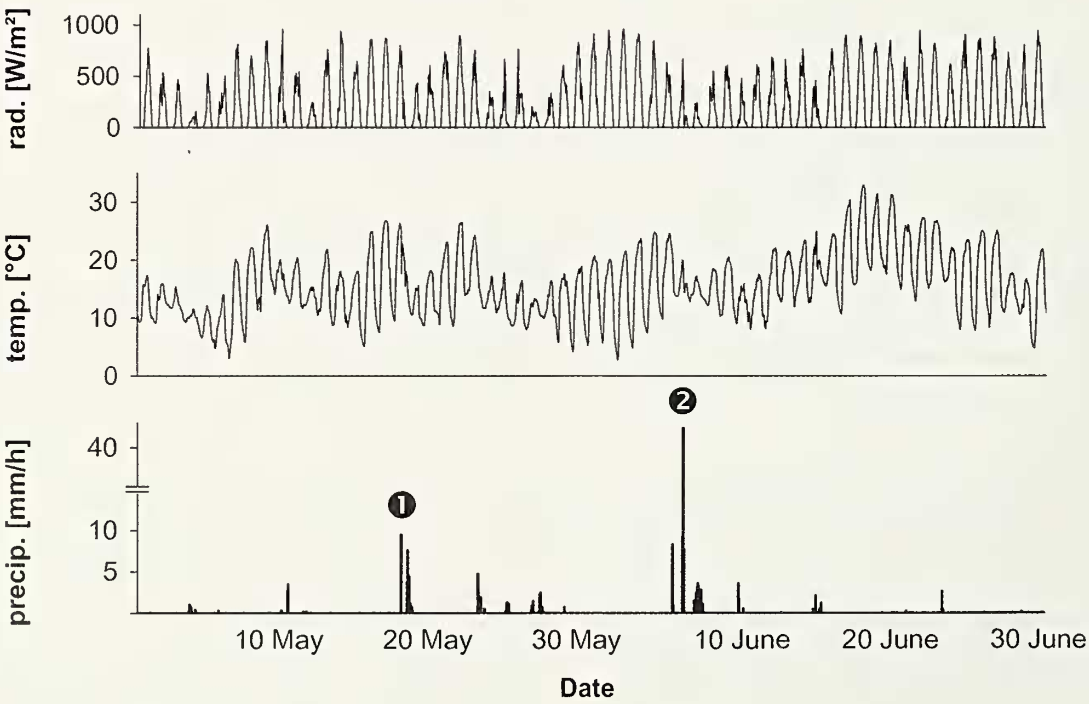

Fig. 1. Climatic conditions (short-wave radiation, temperature, and precipitation) in Bayreuth, May and June 2002. Note the interruption of the y-axis in the lowest graph. Numbers: 1 = raining period during hatching time. 2: heavy rainfall events during instars L2/L3.

the egg mass. Only four colonies built their tent about 30cm above the egg mass. In most cases, the same tent was used (and expanded) over the whole development period. Occasionally (N=6 colonies), caterpillars moved to a web of the ermine moth *Yponomeuta padella* (Linnaeus 1758) (Yponomeutidae) to start tent-building for a second time. Loose *Yponomeuta* webs were sometimes extremely abundant on blackthorn. Such webs were then expanded.

Fifty-two colonies survived until census 7 when the caterpillars had reached their final instar (Table 1). Survival here means that we traced at least one mature caterpillar which we could unequivocally attribute to a given colony. Survival curves varied between sites, but not significantly so (Kaplan-Meier survival analysis: X^2_{3df} =0.50, p=0.92). While on the sites HP, PB and HL no colony became extinct after 9 June 2002, losses of colonies continued to occur at site BB until the end of the larval period. Pooling the data from all sites reveals that mortality occurred almost equally throughout larval development (Fig. 2). We noted somewhat higher incidences of colony failure about 30 days after exposure (i.e., after torrential rainfall of June 6), and from June 12 to June 19 at site BB.

Successful construction of a tent emerged as most crucial factor for the survival of the caterpillars (Fig. 3). Of 24 caterpillar groups that had not been successful in building an initial tent by the second census (i.e. within approximately one week after hatching) 18 became extinct. This amounts to 43.9% of all total losses that occurred after hatching. From the remaining six hatchling groups without a tent only two were able to establish a tent later during the second instar. The other four groups survived without having built a tent, but dwindled to a final group size of only one individual each until census 7. Also later in the larval life, complete destruction of the tent strongly increased the extinction risk of these colonies (Fig. 3). Only two out of 15 colonies that had lost their tent between census 3 and 7 succeeded in rebuilding a tent and two further such colonies survived without a tent, whereas the other eleven colonies died out within 1-3 weeks after tent destruction. Thus, 70.7% of the colony mortality after hatching was caused by or associated with the loss or lack of a tent. Probability of survival was significantly higher (nearly 3-fold) after the successful construction of a tent and again significantly increased (nearly 3-fold) when the tent remained intact or when the caterpillars were able to repair the

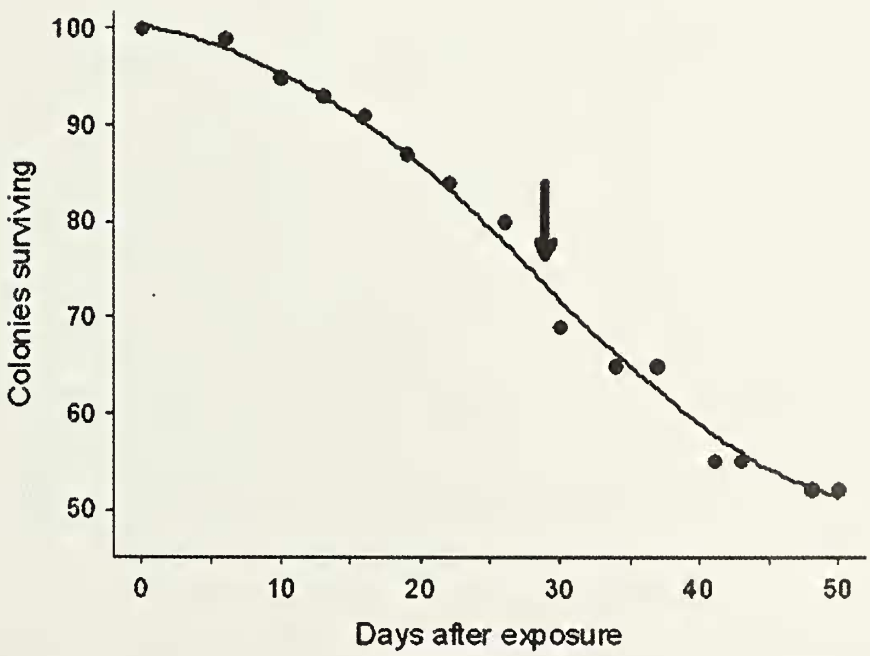

Fig. 2. Number of colonies surviving (initially: n=100 egg batches), summed over the four study sites. Time axis: 0 = exposure day of egg batches. Arrow: day of heavy rainfall. Curve fitted by distance-weighted least-squares regression.

tent before it was totally destroyed (see statistics in Fig. 3).

Although the weekly observations of the colonies provided only snapshots and observations lack completeness, predation was observed by ants (*Lasius* sp., *Formica* sp.), bugs (Miridae), spiders, and beetles (Cantharidae) during the earlier larval stages. Only two of 11 colonies at which predation by invertebrates was directly observed became extinct by the next census. Both these colonies had no tent for their protection. Predation by birds directly at the tents was not noted before census 5 at site HP and census 6 at site BB (i.e. when pre-final instars equipped with urticating hairs were present). None of the tents with obvious damage by birds (N=5) was completely lacking caterpillars, and in no case did bird attacks lead to the complete extinction of a colony.

Heavy rain had a severe impact on the condition of the colonies in our experiments. Fig. 4 shows that all tents at site BB and the majority of tents at the sites HP, PB and HL were damaged after the severe rainfall on June 6. Most tents showed a noticeable reduction of volume at census 5 compared to census 4 and tents were probably temporarily (i.e. until the damage was repaired and the tent was newly expanded again) not habitable for the caterpillars.

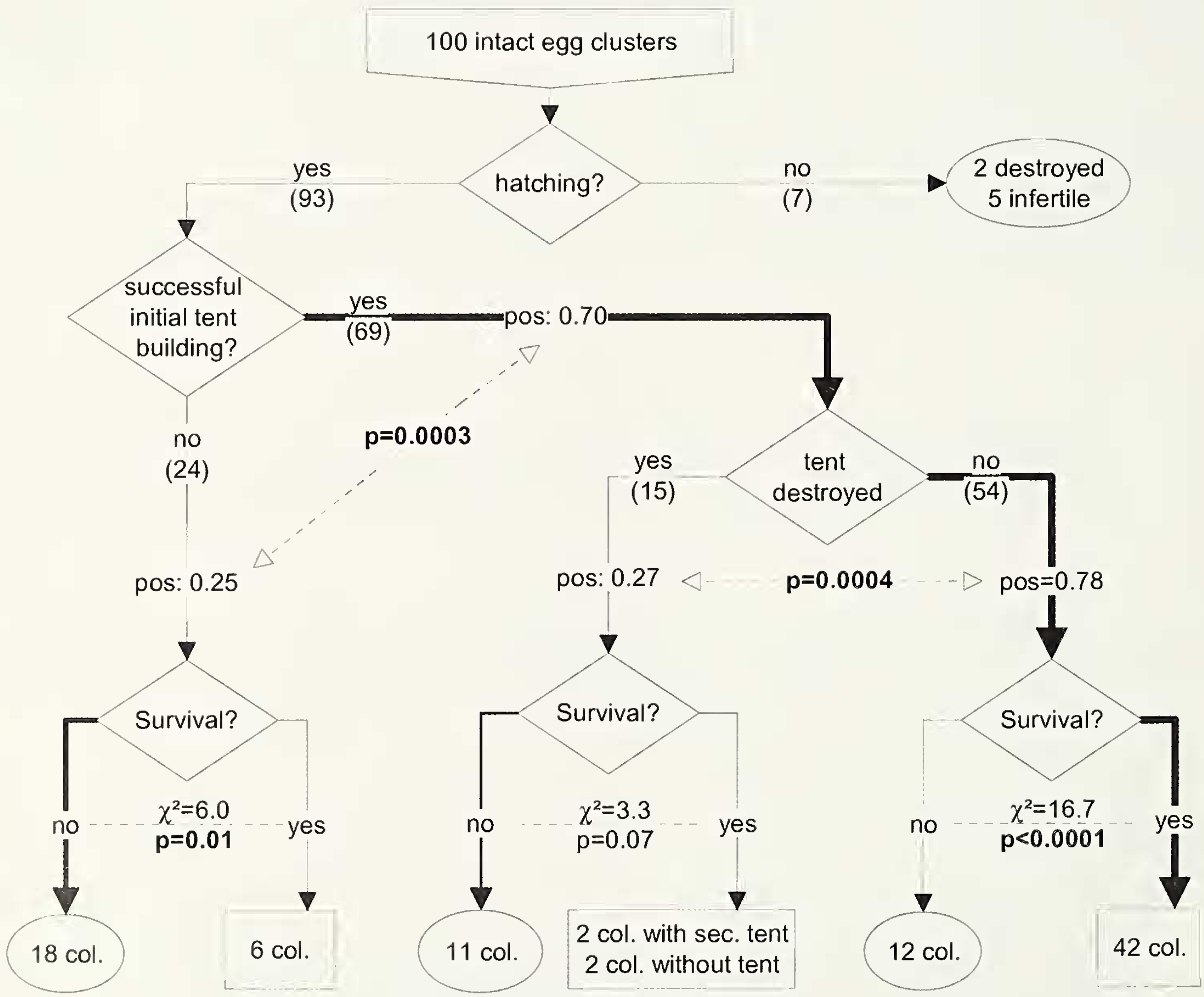

Fig. 3. Flow-chart diagram illustrating the fate of the colonies. Numbers in parentheses = number of colonies. pos = proportion of surviving colonies. Statistics: Comparison of actual survival probabilities at a given point: Fisher's exact test; for deviation of pathways from equal proportions: chi²-test (1df). Probability values printed in bold are significant ($p<0.05$) after sequential Bonferroni correction. Different width of arrows indicates pathways with significant differences in survival.

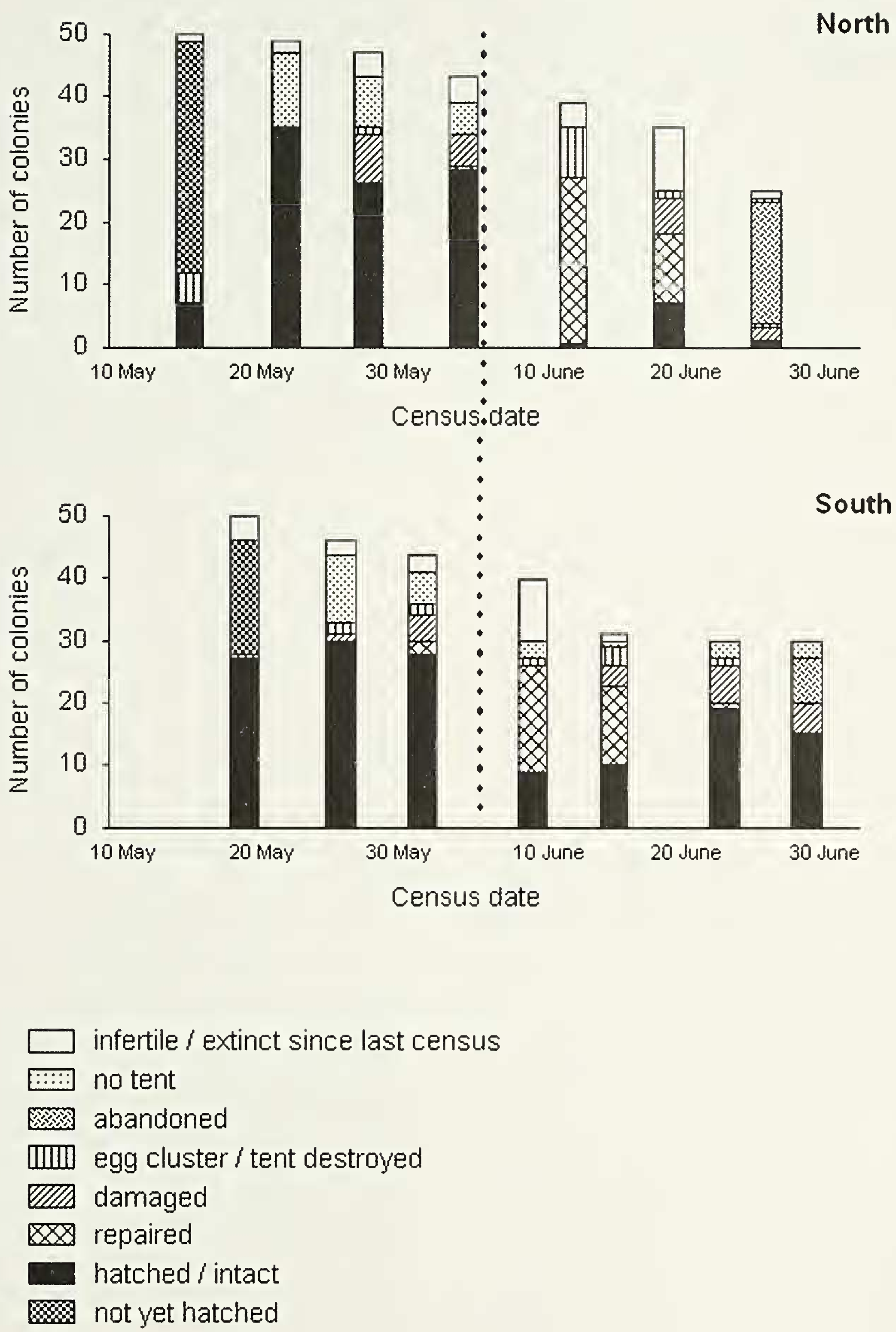

Fig. 4. Condition of colonies during the seven censuses at each site. The dashed line indicates the start of the heavy rainfall that severely damaged most tents. North: Colonies at site BB, South: Colonies at sites HL, HP, PB (these were pooled because of their geographic proximity and to homogenize sample sizes; see Table 1).

Discussion

Colony mortality was not restricted to, nor particularly intense, during early instars in *E. lanestris* in our study, but was rather constant over time. Although older larvae possess defensive urticating hairs, colony mortality did not attenuate in the last two larval stages. Comparable data from other social, tent building caterpillars are rare. In a field study conducted in Georgia, USA, caterpillars of *Malacosoma americanum* finished their development within 7-8 weeks (Costa 1993). Climatic conditions in the Georgia piedmont in March and April and in the region of Bayreuth in May and June are similar with respect to mean temperature (Georgia: March: 13.7°C, April: 16.0°C), whereas precipitation is higher in Georgia (March: 207.5mm, April: 54.6mm; Georgia State Climatology Office 2003).

In contrast to our findings, *M. americanum* experienced significant early-instar mortality but negligible mid- to late-instar mortality. Overall, one third of the *M. americanum* colonies was destroyed by the third to fourth instar but no colony became extinct later on. We assume that the relatively higher mid- and late-instar mortality of *E. lanestris* in our study was predominantly due to the damage of the tents after the heavy rainfall on June 6, which led to the extinction of whole colonies. Climatic conditions did not contribute to mortality in *M. americanum*, perhaps because precipitation was evenly spread without distinct peaks in the year of Costa's (1993) study (i.e. 1990).

Rain seriously affected the constitution of the silk which became brittle leading to large ruptures and holes at the edges of the tent. Additionally, the multiple layers of the tent stuck together after being soaked by heavy rain, which forced the caterpillars to stay outside. Damage at tents may have contributed to higher mortality through facilitation of predation as well as by constraining the tent's thermoregulatory properties (Ruf & Fiedler 2002b).

Climatic factors may also have contributed to first instar mortality. The five day period (15-20 May) with cool weather (daily maximum <20°C) and with substantial precipitation (Fig. 1) most likely constrained mobility of the small caterpillars and retarded the construction of the initial tent just after hatching. Under laboratory conditions (ca. 20°C constantly) without precipitation caterpillars build a tent, in which all caterpillars may hide, within 1-2 days after hatching (C. Ruf, pers. obs.). Besides the direct impact of rain and associated low temperatures which retard mobility, foraging, and digestion (Ruf & Fiedler 2002a), it is very likely that those groups that were not able to build a tent fast enough were decimated by invertebrate predators. As a consequence, too few individuals (10-20) were left which would not be able to construct a tent any more. Those groups are very likely to become extinct.

The impact of weather on the abundance of insects has been analyzed for many species (e.g. Roy et al. 2001 for British butterflies), often showing positive associations with low rainfall. Extreme weather events (e.g. rainstorms) may severely affect butterfly populations, but by their very nature such events lack reproducibility (Dennis & Bardell 1996).

Mortality rates of social caterpillars vary enormously. In two other *Malacosoma* species colony mortality was 40%, or higher than 95%, respectively (Shiga 1979 cited after Fitzgerald 1995; Filip & Dirzo 1985). While our and other studies on social, tent-building caterpillars focused on colony mortality only and not on mortality of individuals, the latter is probably several times higher. In the tent building pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller 1775) (Notodontidae), Schmidt et al. (1990) calculated a mean reduction by 62% of the individuals from the mean number of eggs in a cluster to the mean number of mid-instar caterpillars per colony counted in the field. Unfortunately their study disregarded those colonies that had been completely destroyed between egg deposition and the detection of the colony. Another study on web-building caterpillars (*Hyphantria cunea* (Drury 1773), Arctiidae) found mortality rates of 77-100% during the fourth and fifth stadium by birds and wasps (Morris 1972). Myers (2000) showed that survival of western tent caterpillars (*Malacosoma californicum* (Packard 1864)) varied with the natural 6-11 years periodicity of this species. Highest survival rates were measured in early phases of the population increase and survival was lowest during the population decline. Since our study was confined to one single year, we cannot even guess whether such variation might also occur in *E. lanestris*. However, population cycles have never been reported for *E. lanestris*.

We did not control for the impact of parasitism and virus or bacterial infections on the survival of colonies but no colony showed obvious signs of strong parasitism (e.g. many larval carcasses on the outside of the tents) or disease (heterogeneous multi-instar colonies, shrunken dead caterpillars). Over the years, we observed very few parasitoids emerging from field-collected *E. lanestris* larvae (rates of parasitoid infestation in colonies from site HP <5% in 1999, own unpublished data).

Possession of an intact tent emerged as the strongest predictor of colony success. Overall, 71% of colony failures were related to the loss of the tent. Functions of the tent are numerous (thermoregulation: Joos et al. 1988; Breuer & Devkota 1989; Fitzgerald & Underwood 2000; Ruf & Fiedler 2002b; communication: Fitzgerald & Costa 1999, Ruf 2003; water balance: Wellington 1974). Since caterpillars often rest on the surface of the tents, these structures are expected to be only marginally effective in reducing the overall impact of predators and parasitoids (Fitzgerald 1995), but sophisticated studies controlling for the sole effect of the tent as a refuge from invertebrate predators are missing so far. We suppose that tents serve as a shelter for at least part of the time because many invertebrates (e.g. bugs, wasps, ants) did not enter tents as long as these remained physically intact (C. Ruf, pers. obs.). Destruction of the tent thus means the simultaneous loss of multiple functions enhancing development and communication among the caterpillars. In view of the marked differences in timing and extent of mortaility between species with social caterpillars (see above), it is quite likely that the relative importance of various mortality risk factors differs between species and also depends on population density.

Silken tents are a costly investment for herbivorous caterpillars (Berenbaum et al. 1993; Craig et al. 1999; Stevens et al. 1999). The importance of the tent is obvious since *E. lanestris* caterpillars repaired the tent whenever it had been destroyed but normally did not leave it. The only cases where a replacement of the tent was observed were associated with the expansion of an already existing *Yponomeuta* web, thus saving costs for a completely new tent.

In a meta-analysis comparing published survival curves for gregarious and solitary Lepidoptera and Symphyta, Hunter (2000) showed that gregarious caterpillars are less likely to die during the earlier instars than solitary caterpillars, but mortality rates rise during the later development (last, solitary instars, pupal phase). Overall, in the comparative analysis survival (from egg to adult) was not significantly different between solitary and gregarious species whereas the timing of mortality differed between the two classes. Our data conform to this pattern, with rather low rates of colony failures during early stages, and slightly more frequent losses later on.

In highly social caterpillars, where tent-building can only be achieved by large numbers of cooperating siblings, colony mortality reduces a female's individual fitness to zero even though mean survival may be high on the population level. Thus, there must be a strong trade-off for tent-building in highly social Lepidoptera between high benefits, primarily by developmental advantages, and high costs due to the risk of complete reproductive failure. Most mature *E. lanestris* tents we found in the field contained more than 200 larvae. Since the mean fecundity of an *E. lanestris* female is about 325 eggs (Ruf et al. 2003) survival must be quite high once the hatchlings have established their tent and no extreme weather events influence the caterpillars' development. Thus, in *E. lanestris* the benefits of sociality usually outweigh the high risk of losing the whole offspring. As we have shown here, possession of an intact tent plays the most important role in that regard.

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